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Tempo and mode in human evolution

(*Australopithecus*/*Homo*/phylogeny/bipedalism/encephalization)

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ABSTRACT The quickening pace of paleontological discovery is matched by rapid developments in geochronology. These new data show that the pattern of morphological change in the hominid lineage was mosaic. Adaptations essential to bipedalism appeared early, but some locomotor features changed much later. Relative to the highly derived postcrania of the earliest hominids, the craniodental complex was quite primitive (i.e., like the reconstructed last common ancestor with the African great apes). The pattern of craniodental change among successively younger species of Hominidae implies extensive parallel evolution between at least two lineages in features related to mastication. Relative brain size increased slightly among successively younger species of *Australopithecus*, expanded significantly with the appearance of *Homo*, but within early *Homo* remained at about half the size of *Homo sapiens* for almost a million years. Many apparent trends in human evolution may actually be due to the accumulation of relatively rapid shifts in successive species.

In the 50 yr since the publication of Simpson's *Tempo and Mode in Evolution* (1) the paleontological record of Hominidae has improved more than a 100-fold. The improvements include precise geological dating and rich collections of well-preserved fossil hominids. Particularly valuable are newly discovered postcranial remains of early species that permit body-size estimation (2–4). These new data show that the pattern of morphological change in the hominid lineage was mosaic. Different parts of the body evolved at different times and at various rates. This report focuses on hominid phylogeny and the tempo and mode of evolution of bipedalism, the hominid dental configuration, and encephalization.

Species, Clades, and Phylogeny

Views differ on the definitions of fossil hominid species and their phylogenetic relationships for many reasons but especially because of (i) the difficulty in identifying paleospecies (5–8) and (ii) the pervasiveness of homoplasy (9). One view (9) consists of five species of *Australopithecus* (*A. afarensis*, *A. aethiopicus*, *A. africanus*, *A. boisei*, and *A. robustus*) and three of *Homo* (*H. habilis*, *H. erectus*, and *H. sapiens*). Table 1 presents the geological dates and the estimated body, brain, and tooth sizes of these species.

Analysis of the states of 77 craniodental characters in these species of *Australopithecus* and *H. habilis* (9) reveals that the cladogram in Fig. 1A is the most parsimonious (tree length = 12,796, consistency index = 0.72). The two late “robust” australopithecines, *A. robustus* and *A. boisei* are the most highly derived and form a sister group with early *Homo*. This branch links with *A. africanus* to form a clade containing *A.*

africanus, *A. robustus*, *A. boisei*, and early *Homo*. *A. aethiopicus* branches from this clade next with *A. afarensis* as a sister species to all later hominids.

Fig. 1B displays the phylogenetic tree implied by the most parsimonious cladogram. This phylogeny implies that *A. afarensis* is the most primitive hominid and that all later hominids shared a common ancestor that was more derived than *A. afarensis*. This post-*afarensis* hypothetical ancestor may someday be discovered. Its morphology can be reconstructed by observing the many ways *A. aethiopicus* resembles later hominids (especially *A. africanus*) and not *A. afarensis*. For example, the canine eminences of the face are prominent in the outgroup and in *A. afarensis* but are reduced or absent in all other species of hominid, which implies that the common ancestor of all post-*afarensis* species had canine eminences that were also reduced. This hypothetical ancestor would have a strongly developed metaconid on the lower first premolar. It would not, however, resemble *A. aethiopicus* in traits related to masticatory hypertrophy (heavy chewing), nor would it resemble any other post-*afarensis* species because they are all too derived in flexion of the base of the skull, orthognathism (flat faced), and encephalization to have been the ancestor of *A. aethiopicus*. After the divergence of *A. aethiopicus*, this phylogeny depicts a common ancestor of *A. africanus*, *A. robustus*, *A. boisei*, and *Homo* that resembled *A. africanus* in its development of anterior dentition, basicranial flexion, orthognathism, and encephalization. A second hypothetical common ancestor appears in Fig. 1B to account for the numerous derived traits shared by *A. robustus*, *A. boisei*, and early *Homo* that are not seen in *A. africanus*. This ancestor would have the degree of basicranial flexion and orthognathism seen in early *Homo* and the amount of encephalization seen in *A. robustus* and *boisei*. This phylogeny proposes a third hypothetical ancestor that would be at the root of the lineage leading to *A. robustus* and *A. boisei*. This ancestor probably resembled *A. robustus* in traits related to heavy chewing.

Although the most parsimonious cladogram implies this phylogeny, other cladograms are possible but less probable. A cladogram linking *A. aethiopicus* to *A. boisei* and *robustus* as one branch and *A. africanus*/early *Homo* as another requires more evolutionary steps (tree length = 13332; consistency index = 0.69) because the later “robusts” resemble early *Homo* in so many features. These features include many aspects of basicranial flexion, loss of prognathism (muzzle), changes in the anterior dentition, and encephalization. The postcrania, although not included in this analysis, support the view that at least *A. robustus* and early *Homo* are monophyletic relative to other species of early hominid.

Whatever the true phylogeny is, and there can be only one, the fact remains that homoplasy is commonplace. Some resemblances appeared independently and not because of

Table 1. Species of *Australopithecus*, *Homo*, and modern African apes with geological ages, estimated body weights, brain volumes, relative brain sizes (EQ), cheek-tooth area, and relative cheek-tooth area (MQ)

Species	Dates, Myr	Body weight, kg*		Brain volume,† cm³	EQ‡	Tooth area,§ mm²	MQ¶
		Male	Female				
<i>A. afarensis</i>	4–2.8	45	29	384	2.2	460	1.7
<i>A. africanus</i>	3–2.3	41	30	420	2.5	516	2.0
<i>A. aethiopicus</i>	2.7–2.3			399		688	
<i>A. boisei</i>	2.1–1.3	49	34	488	2.6	756	2.5
<i>A. robustus</i>	1.8–1.0	40	32	502	2.9	588	2.2
<i>H. habilis</i>	2.4–1.6	52	32	597	3.1	502	1.7
Early <i>H. erectus</i>	1.8–1.5	58	52	804	3.3	377	1.0
Late <i>H. erectus</i>	0.5–0.3	60	55	980	4.0	390	1.0
<i>H. sapiens</i>	0.4–0	58	49	1350	5.8	334	0.9
<i>Pan paniscus</i>	0	38	32	343	2.0	227	0.9
<i>Pan troglodytes</i>	0	49	41	395	2.0	294	0.9
<i>Gorilla gorilla</i>	0	140	70	505	1.7	654	1.0

*See refs. 2 and 10.

†Endocranial volume is transformed into brain volume by formula 4 in ref. 11.

‡Expected brain volume is $0.0589 (\text{species body weight in g})^{0.76}$; see ref. 12.§Tooth area is the sum of the $\text{md} \times \text{bl}$ diameters of P₄, M₁, and M₂; see ref. 13.¶MQ, ratio of observed tooth area and expected area; expected area is $12.15 (\text{species body weight in kg})^{0.86}$; see ref. 13.||Two species may be represented in this sample. Using Wood's 1988 classification, I calculate the values for *H. habilis sensu stricto* and *Homo rudolfensis* as follows: male body weight, 37 and 60 kg; female body weight, 32 and 51 kg; brain volume, 579 and 709 cm³; EQ, 3.5 and 3.0; tooth area, 478 and 570 mm²; MQ, 1.9 and 1.5 kg; see ref. 10.

evolution from a common ancestor that possessed the same feature. Either adaptations for heavy chewing evolved twice or basicranial flexion, orthognathism, reduced anterior dentition, and encephalization each evolved more than once.

Bipedalism and the Postcranium

However the specific phylogeny of Hominidae is reconstructed, the important point is that these species are closely related to *H. sapiens*, and, in general, the more recent in time

the species is, the more derived features it shares with our species. The earliest species, *A. afarensis*, is the most primitive in the sense that it shares the fewest of these derived traits and retains a remarkable resemblance to the common ancestor of African apes and people in many craniodental features. Its postcranium, however, is highly derived (14). It is fundamentally reorganized from that typical of apes to that specific to Hominidae (14–24).

Fig. 2 presents features in which the postcranium of *A. afarensis* differs from African apes and approaches the

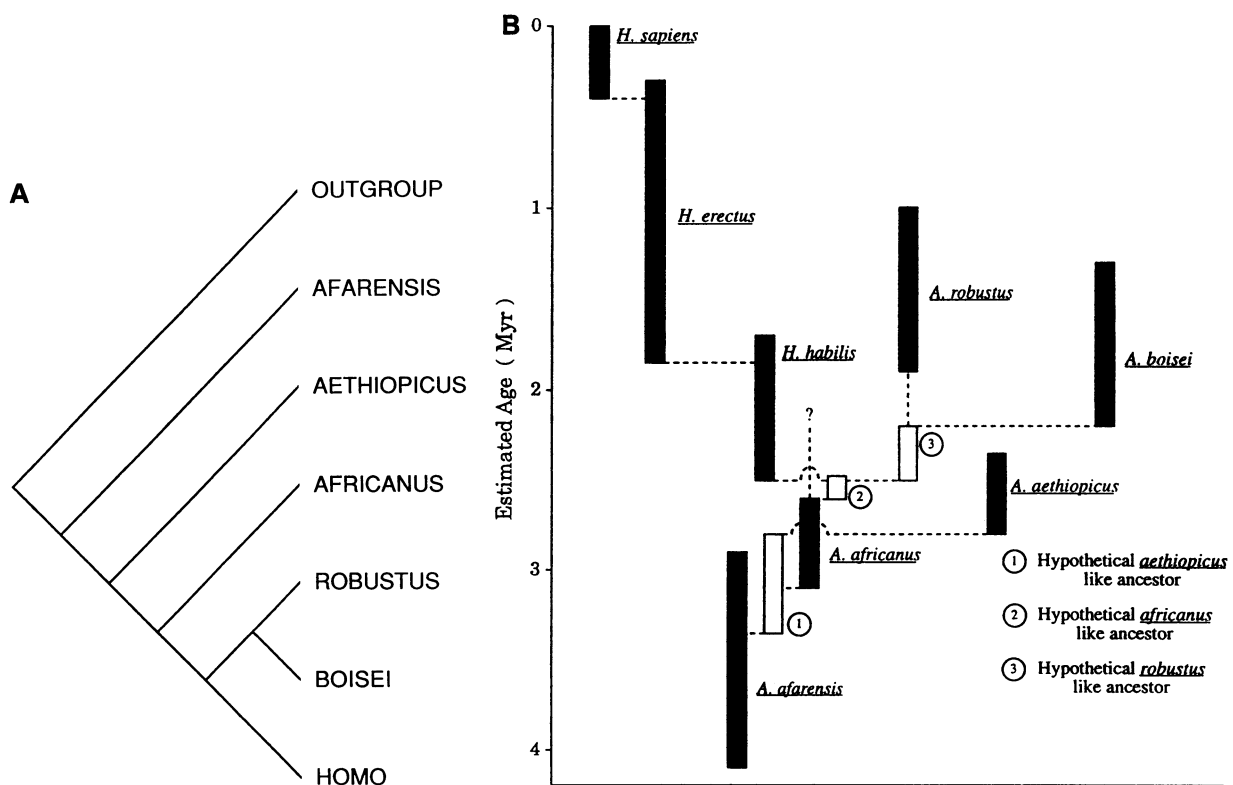


FIG. 1. (A) The most parsimonious cladogram using all 77 traits or using summary scores from the analyses of five functional complexes or seven anatomical regions. Tree length is 12,796 and consistency index is 0.722. (B) The phylogeny implied by the most parsimonious cladogram. Three hypothetical ancestors are predicted.

Lumbar lordosis and sacral retroflexion

Sacral ala expanded laterally

Sacroiliac and hip joints closely approximated

Pelvis with:

- Mediolaterally expanded, superoinferiorly shortened, and anteriorly rotated iliac blades
- Robust anterior iliac spines
- Distinct sciatic notch
- Distinct iliopsoas groove
- Rugose and large area for sacrotuberous ligament
- Retroflexed auricular surface with extensive retroauricular area
- Robust posterior superior iliac spine
- Sigmoid curvature of iliac crest
- Dorsoventrally thickened pubic symphysis
- Retroflexion of hamstring tuberosity
- Shortened ischial shank

Femoral neck long with human-like distribution of cortical and spongy bone

Distal femur with:

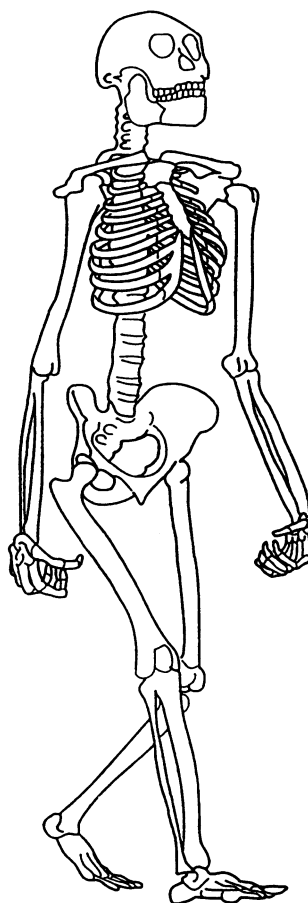
- High bicondylar angle
- Elliptical lateral condyle
- Deep patellar groove with high lateral lip

Calcaneus with:

- Massive body
- Deep dorsoplantar dimension
- Ovoid transverse section
- Horizontally oriented sustentacular shelf

Midtarsal region is:

- Stout
- Anteroposteriorly expanded
- Strong transverse and longitudinal arch



Relative small forelimbs

Proximal humerus with open and shallow bicipital groove

Distal humerus with:

- Rounded lateral well of olecranon fossa
- Gracile lateral epicondyle
- Moderate-sized and cranially facing medial epicondyle
- Moderate development of supracondylar ridge

Radiocarpal joint perpendicular to shaft axis

Capitate with:

- Proximodistally shortened axis
- Single and elongated facet for MCII
- Shallow excavations for MCIII articulations

Metacarpals II-V relatively short with no dorsal transverse ridge on heads

Phalanges relatively short

Tibia with straight shaft

Distal tibia with articular surface nearly perpendicular to shaft axis

Metatarsal I with:

- Robust and triangular diaphysis
- Expanded head

Metatarsals II-V with:

- Heads expanded superiorly
- MTV powerfully built with large tuberosity

Hallux is convergent

Toes relatively short

Proximal phalanges with dorsally oriented proximal articular surfaces

FIG. 2. Derived postcranial traits shared by *A. afarensis* and *H. sapiens*. MC, metacarpal. MT, metatarsal

condition characteristic of humans. The most significant features for bipedalism include shortened iliac blades, lumbar curve, knees approaching midline, distal articular surface of tibia nearly perpendicular to the shaft, robust metatarsal I with expanded head, convergent hallux (big toe), and proximal foot phalanges with dorsally oriented proximal articular surfaces. A commitment to bipedalism in *A. afarensis* is also shown by the 3.5 million year (Myr) Laetoli footprints, which show very human-like proportions, arches, heel strike, and convergent big toes (24–27).

The nature of *A. afarensis* implies that bipedalism evolved well before the appearance of most other hominid characteristics. The appearance of bipedalism is sudden in the sense that it involved a complex alteration of structure in a relatively short period of time. Unfortunately, the fossil record does not yet include hominid postcrania predating 4.0 Myr that would document the transition from ape-like to hominid locomotion. The fundamental changes had already taken place in *A. afarensis*.

These bipedal alterations seen in *A. afarensis* are incomplete relative to modern *H. sapiens*, however (23, 28–40). Fig. 3 presents traits in which this species differs in its

postcranium from later species of Hominidae. These plesiomorphies probably imply that the bipedalism of *A. afarensis* was kinematically and energetically different from modern humans and may imply that they were more efficient tree climbers than modern humans. This arborealism would have been different from ape-like tree climbing, however, because the hindlimb was specialized for bipedality and had lost essential climbing adaptations such as hallucial divergence.

The pattern of change in these traits in later species of Hominidae is complex. Most of the postcranial elements that can be directly compared reveal a period of stasis with no change between *A. afarensis* and *A. africanus* (23, 32). This is particularly striking in the capitate bone in the wrist and pelvis. Both have the identical combination of modern pongid, modern human, and unique characteristics. In the metacarpals and hand phalanges, however, *A. africanus* has some *Homo*-like features absent in *A. afarensis* (41, 42). The distal thumb phalanx of *A. africanus*, for example, is very human-like with its broad apical tuft that contrasts sharply with the relatively narrow, chimp-like tufts of the distal phalanges of *A. afarensis*. Limb proportions remain similar to *A. afarensis* in all species until the appearance of *H. erectus*

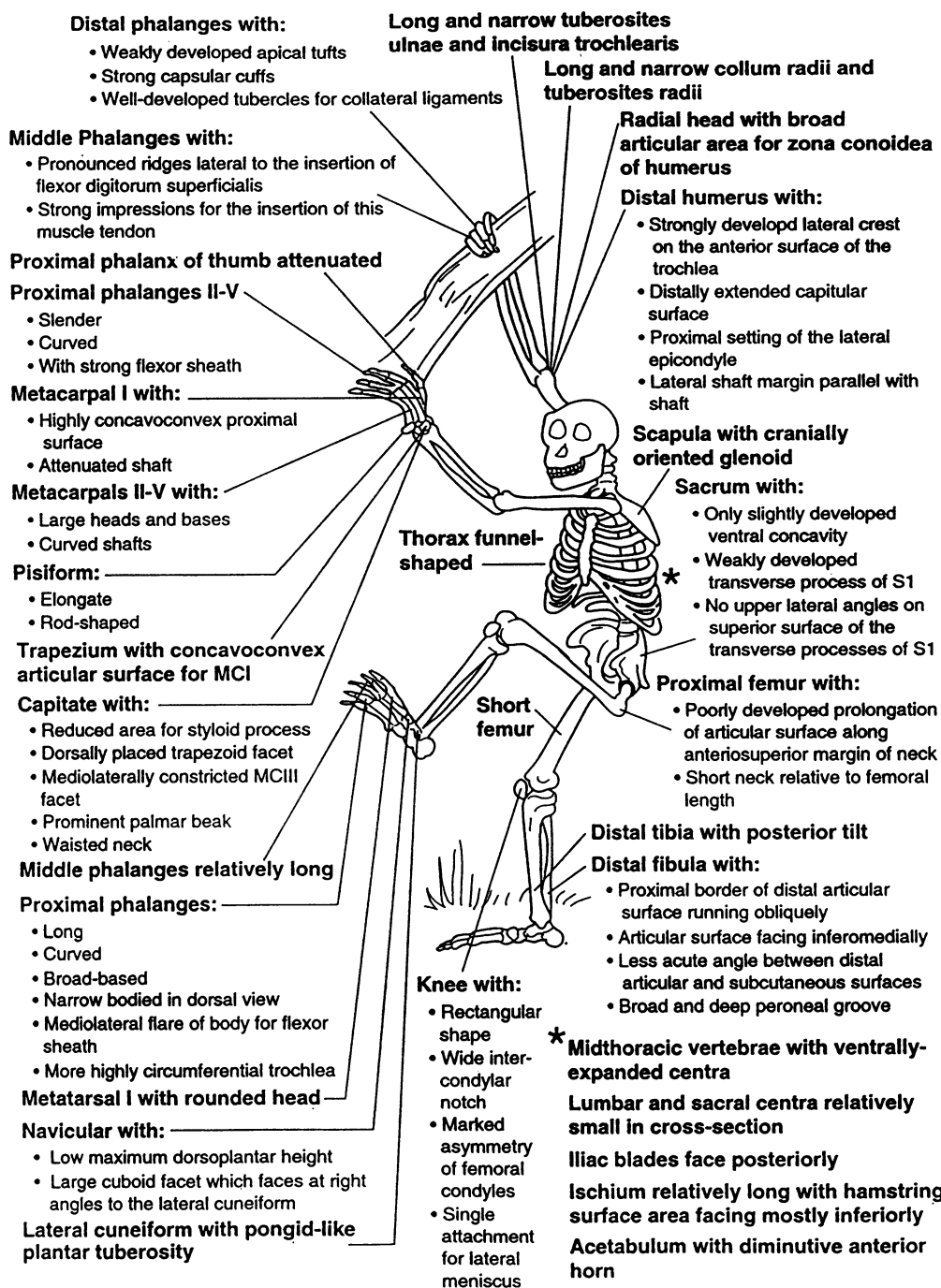


FIG. 3. Primitive postcranial traits of *A. afarensis* shared with the reconstructed common ancestor of African apes and humans. MC, metacarpal.

at 1.7 Myr (2). Even *H. erectus* retains some primitive characteristics relative to *H. sapiens* (7). The most conspicuous of these is the relatively small cross-sectional area of the lumbar and sacral bodies (43). Narrow pelvic inlets and long femoral necks are characteristic of *A. afarensis*, *A. africanus*, and *H. erectus* and are probably related to parturition of smaller-head neonates (21, 44–49).

Body size remains relatively small in all species of *Australopithecus*, including the surprisingly petite bodies of the “robust” australopithecines (refs. 2–4, 49; Table 1, column 3). Sexual dimorphism in body size decreases from *A. afarensis* to *A. africanus* to *A. robustus*. Specimens attributed to *H. habilis* vary enormously in size and may imply (with other evidence) the existence of two species (3, 10, 14,

50). A sudden change occurs at 1.8 Myr with the appearance of *H. erectus* with body weights as high as 68 kg and a substantial reduction in sexual dimorphism. There is no evidence of a gradual trend of increased body weight through time, as might be expected from Cope’s law.

Mastication

The distinction between the hominid and pongid dental pattern was sharply delineated before the discovery of *A. afarensis* (51), but that species bridged the gap (52, 53). Overall, the dentition of the earliest species of hominid is more similar to the inferred last common ancestor than it is to *H. sapiens*. Most notable primitive traits include large

central and small lateral upper incisors, projecting upper canine with marginal attrition facets, small metaconid of the lower first premolar and parallel or convergent tooth rows. The positions of the masticatory muscles are also primitive, particularly the posterior placement of the main fibers of the temporalis. But there are numerous derived features shared with later hominids as well. The most conspicuous of these is the reduced canines with apical wear.

Hominid species postdating *A. afarensis* lose this species' primitive dental characteristics. *A. africanus* is variable in size and shape of its anterior teeth, but some specimens are more *Homo*-like (5, 50). Its lower first premolar is decidedly bicuspid. The mass of the temporalis muscle has moved forward into a more *Homo*-like position. Prognathism is reduced. The primitive dental features of *A. afarensis* are lost in hominid species postdating the appearance of *A. africanus*.

One unexpected characteristic of all early hominid species is postcanine megadontia and associated features related to heavy chewing (9, 13, 54–63). Relative to body size, the cheek-teeth of *A. afarensis* are 1.7 times larger than expected from that seen in modern species of Hominoidea (Table 1, column 8). Relative cheek-tooth size is higher in *A. africanus* (2.0) and higher still in *A. robustus* (2.2) and *A. boisei* (2.5). The appearance of *Homo* is marked by a reduction to 1.7. From the earliest *Homo* species to *H. erectus* to *H. sapiens* there has been dental reduction. Presumably the masticatory hypertrophy within species of *Australopithecus* is related to diet and to the amount of grit entering the mouth. Reduction of tooth size in *Homo* may reflect dietary change, but also it is probably related to the use of tools in preparing food.

The phylogeny presented in Fig. 1B implies traits related to heavy chewing evolved by parallel evolution in two lineages. One of these is the lineage from *A. afarensis* to *A. aethiopicus*. The second is the lineage from *A. afarensis* to *A. africanus* to the late "robust" australopithecines, *A. robustus* and *A. boisei*. This is a surprising result because *A. aethiopicus* and *A. boisei* share a suite of unique character states such as extreme anterior projection of the zygomatic bone, huge cheek teeth, enormous mandibular robusticity, a heart-shaped foramen magnum, and temporoparietal overlap of the occipital at asterion (at least in males).

All of these traits, except for the heart-shaped foramen magnum, are related to the functional complex of heavy chewing. The huge cheek-teeth and robust mandibles of both species are obviously part of masticatory hypertrophy. The

anterior projection of the zygomatic bones brings the masseter muscles into a position of maximum power. The encroachment by the root of the zygomaticoalveolar crest obscures the expression of the anterior pillars and upper canine jugae. Even the morphology of the temporoparietal overlap with occipital is related to the function of the forces generated by the chewing muscles (9).

Theoretically, it is understandable how such detailed similarity could be due to parallel evolution. These species are closely related and share "... so much in common in their constitution" (64) that similar selective forces produce similar morphologies. The selective forces in this case are related to a feeding adaptation that is associated with a specialized ecological niche. As Mayr (ref. 65, p. 125) points out "... most adaptations for special niches are far less revealing taxonomically than they are conspicuous. Occupation of a special food niche and the correlated adaptations have a particularly low taxonomic value." In fact, many of the same traits characteristic of *A. aethiopicus* and the other "robust" australopithecines reappear in distantly related species adapted to heavy chewing. Expansion of the cheek-teeth, shortening of the muzzle, and anterior migration of the attachment areas of the chewing muscles are seen in other primates whose diet requires heavy chewing (e.g., *Hadropithecus*, *Theropithecus*, probably *Gigantopithecus*, and *Ekmowehashala*).

Encephalization

Table 1, column 5 presents brain sizes in species of Hominoidea. Absolute brain volume has more than tripled from *A. afarensis* to *H. sapiens*, and relative size has more than doubled (6, 8, 11, 12, 22, 66–84). Given the very human-like postcranium of *A. afarensis*, it is interesting that this species has a relative brain size very close to that of modern chimpanzees. Lamarck, Huxley, Haeckel, and Darwin speculated that bipedalism preceded encephalization, but they had no fossil proof (78). The early species of *Australopithecus* confirm their prediction.

Both absolute and relative brain size increase through time in the series from *A. afarensis* [384 cc, 2.2 ratio of brain volume and expected volume (EQ)] to *A. africanus* (420 cc, 2.5 EQ) to *A. boisei* (488 cc, 2.6 EQ) to *A. robustus* (502 cc, 2.9 EQ). Superficially, this increase through time appears to be by gradual increments, but samples are small and body

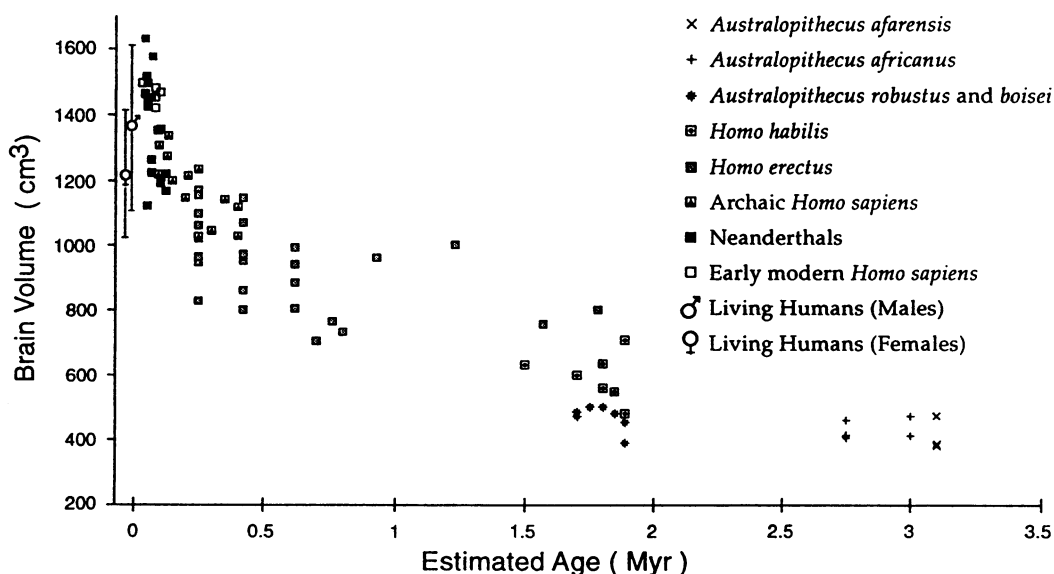


FIG. 4. Brain size (in cm³) plotted against time (Myr) for specimens attributed to Hominidae.

weight determinations are inexact (2). The sample of endocasts of *A. afarensis* consists of three specimens and of these, all are fragmentary, and one is the estimated adult size from a 2.5-yr-old child (68). Although there are six endocasts of *A. africanus*, three of these needed substantial reconstruction (74). There is only one endocast of *A. robustus*, four of *A. boisei*, seven of *H. habilis*, five for early *H. erectus*, and five for late *H. erectus*. Body weight estimates may be off the mark, but the sample of postcranial specimens is sufficient to show that body weight remained at about the same relatively small size in all species of *Australopithecus*. This result implies that the apparent increase in brain size through time in species of *Australopithecus* is not due merely to an increase in body size. Body size and brain size are variable in specimens attributed to *H. habilis* with individuals as small as 32 kg and 484 cc and others as large as 57 kg and 709 cc. Although there are reasons to keep *H. habilis* as a single species (6), dividing the sample into two species is justifiable (8, 50). With either taxonomy, the absolute brain sizes of these early *Homo* specimens lie between *Australopithecus* and *H. erectus*, although relative brain sizes of early members of *H. erectus* overlap the range of the smaller-bodied specimens of *H. habilis*. The relative brain size of early *H. erectus* is surprisingly small because body size is so large. By 1.7 Myr, individuals attributed to *H. erectus* grew to >180 cm, and by 1.5 Myr one individual (KNM-WT 15000) may have stood 185 cm and weighed 68 kg as an adult (4). Despite the fact that the average early *H. erectus* brain was >200 cc larger than the average brain of *H. habilis*, the relative brain sizes are only slightly different ($EQ = 3.1$ and 3.3).

The pattern of encephalization since early *H. erectus* is difficult to interpret because geological dates are less accurate, variability is high, and body weights are difficult to establish. Fig. 4 plots brain size against time. For its first million years, *H. erectus* has absolute brain volumes that do not increase through time and therefore represent a period of stasis (85). It is difficult to establish whether relative brain sizes increased because there are very few postcranial fossils of *H. erectus* after 1.5 Myr from which to estimate body size. The few femora that are known are similar in size to those from early *H. erectus*. When taken over its entire range, the current sample of *H. erectus* does show a weak, but significant, positive increase in brain size through time (76). The sample of archaic *H. sapiens* (0.4–0.125 Myr) shows a strong positive trend (76). Variability is high. Many specimens as old as 0.4 Myr are within the modern human range of variation, and after 0.25 Myr all specimens are within this range. The average for the Neanderthals is 1369 cc compared with 1462 cc for early modern *H. sapiens*.

Stasis, Punctuation, and Trends

It is useful to regard evolutionary change in the hominid lineage from the point of view of Mayr's peripatric theory of speciation (86). Presumably, most of our samples derive from central populations of species and not from the small, isolated, and peripheral groups that are the most likely source of new species. When one of these peripheral isolates becomes reproductively isolated from the central species and its geographical range expands, it may overlap with the parent species, resulting in the coexistence of ancestral and descendant species. As depicted in Fig. 1B, ancestral species overlap in time with descendants in most cases in hominid evolution, which is not what would be expected from gradual transformations by anagenesis (87). Trends through time observed in the fossil record are not necessarily the result of gradual change but rather "... an accumulation of discrete speciation events" (ref. 86; p. 223).

These events can be obscured by defining paleospecies too broadly, however. For example, it is conventional to define

H. erectus as including specimens from deposits as old as 1.8 Myr and as young as 0.2 Myr (85). There is a slight trend in brain-size increase in this series (76), but the earliest and smallest brained specimens are regarded by some as a separate species, *Homo ergaster* (50, 88, 89). Another example is the inclusion of specimens into *H. sapiens* that date back to perhaps 0.5 Myr, despite their decidedly archaic features. By this attribution, there is a strong positive trend in brain size through time (76). An argument can be made, however, that this sample consists of several species (90).

This view does not exclude the presence of change through time within species, however. As the original proponents of the theory of punctuated equilibrium point out (86), this view concerns the relative frequency of stasis, punctuation, and phyletic gradualism. Even within the multiple-species hypothesis of Middle to Late Pleistocene *Homo* (90), all change through time does not occur at speciation events. For example, brain size and cranial morphology change from early to late specimens referred to *Homo neanderthalensis*. It is interesting, however, how little change occurs within most hominid species through time.

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